

FIRST OCCURRENCE OF *SEYMOURIA*  
(AMPHIBIA: BATRACHOSAURIA) IN THE  
LOWER PERMIAN ROTLIEGEND OF  
CENTRAL GERMANY

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ABSTRACT

The amphibian *Seymouria* is reported for the first time from outside of the Lower Permian of North America. Two specimens that include skulls and some postcrania are described from the Lower Permian Tambach Formation, lowermost unit of the Upper Rotliegend, of the Bromacker locality in the middle part of the Thuringian Forest near Gotha, central Germany. They are tentatively referred to *S. sanjuanensis*, known otherwise only from Lower Permian deposits of Wolfcampian age in southwestern United States. The *Seymouria* and several other tetrapods from the Bromacker locality form an assemblage that is found elsewhere only in the Lower Permian of the United States. The Bromacker tetrapod assemblage is, therefore, of great importance not only in assessing the biostratigraphic position and age of the Tambach Formation, but also in reconstructing distribution patterns of Early Permian vertebrates.

INTRODUCTION

Until very recently, all well-documented occurrences of the well-known amphibian *Seymouria* were restricted to the Lower and lowermost Upper Permian of the southwestern United States. The first described and most commonly encountered species, *S. baylorensis* Broili (1904), occurs mainly in the middle Leonardian age deposits of the lowermost horizon of the Clear Fork Group (Arroyo Formation) of north-central Texas. A detailed knowledge of the anatomy of *Seymouria* is based almost entirely on the description of this species by Watson (1918) and White (1939). On the basis of a dozen specimens, including skulls and partial postcrania, collected from the earlier deposits of the late Wolfcampian (earliest Permian) age Organ Rock Shale, Cutler Group of southeastern Utah, Vaughn (1966) described a second species, *S. sanjuanensis*. Six additional specimens of *S. sanjuanensis*, some essentially complete and all preserved in a single block from an early to middle Wolfcampian horizon in the Lower Permian Cutler Formation of north-central New Mexico, were described by Berman et al. (1987). Two other species of *Seymouria* have been described on the basis of poorly preserved and limited materials: *S. grandis* Olson (1979) from a late Leonardian age horizon of the Clear Fork Group (Vale Formation) of north-central Texas and *S. agilis* Olson (1980) from a lowermost horizon of the Upper Permian, Guadalupian age Flowerpot Formation of Oklahoma. A greater geographic distribution of *Seymouria* was noted by Langston (1963), who reported its occurrence in the Lower Permian red beds of Prince Edward Island of eastern Canada. Identification

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was based on a small, partial right femur he believed to be indistinguishable from that of *S. baylorensis*.

In a series of papers Martens (1988, 1989) and Boy and Martens (1991) reported a diverse assemblage of tetrapods (amphibians and reptiles) that are represented by articulated skeletal remains, as well as some invertebrates (conchostracans, insects, and myriapods) from a single site in the Lower Permian red-bed deposits of the Upper Rotliegend of Germany. The site, an abandoned sandstone quarry known as the Bromacker locality, is in the middle part of the Thuringian Forest, central Germany. The presence of vertebrate skeletal remains at the Bromacker locality was only recently discovered by Martens in 1974 (Martens, 1980). Two of the vertebrate specimens found at the Bromacker locality are described here as belonging to the amphibian genus *Seymouria*, and each includes a skull and some postcranial elements. The larger and better preserved of the two, which was earlier assigned to *Seymouria* by Martens (1988, 1989), is nearly indistinguishable from *S. sanjuanensis* from the Lower Permian of Utah and New Mexico (Vaughn, 1966; Berman et al., 1987).

The *Seymouria* reported here is part of a growing assemblage of terrestrial or semi-terrestrial tetrapods from the Bromacker locality that on the one hand is unique for western and central Europe, but on the other is quite typical of that found in widely separated Lower Permian deposits in the United States. The resemblance between the Bromacker and the United States tetrapod assemblages most likely reflects a similarity in environmental conditions, inasmuch as the sediments of the Bromacker locality, as well as the Upper Rotliegend in general, include typical fluvial red-bed facies like those in the Lower Permian of the United States (Martens, 1975, 1982, 1988, 1989; Martens et al., 1981). The Bromacker vertebrate assemblage, therefore, provides a unique opportunity to understand better the distributional patterns of Early Permian vertebrates across northern Pangaea.

The following abbreviations are used to refer to collection repositories: CM, The Carnegie Museum of Natural History, Pittsburgh; CNHM, Field Museum of Natural History, Chicago; MCZ, Museum of Comparative Zoology, Harvard; MNG, Museum of Nature, Gotha, Germany; NTM VP, Navajo Tribal Museum, Window Rock, Arizona; and TMM, Texas Memorial Museum, University of Texas, Austin.

Abbreviations used in figures are as follows: an, angular; art, articular; bps, basiparasphenoid complex; cl, clavicle; co, coronoid; d, dentary; f, frontal; il, ilium; it, space for intertemporal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pc, palpebral cup; pf, postfrontal; pm, premaxilla; po, postorbital; pra, prearticular; prf, prefrontal; psp, postsplenial; pt, pterygoid; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal; st, supratemporal; v, vomer.

#### GEOLOGY

The *Seymouria* specimens described here, as well as a variety of other tetrapods described or noted by Martens (1988, 1989) and Boy and Martens (1991), are from the Lower Permian Tambach Formation, Upper Rotliegend, of the Bromacker locality near the village of Tambach-Dietharz and about 20 km south of the town of Gotha in the middle part of the Thuringian Forest, central Germany (Fig. 1). The Bromacker locality has been long known as a very important locality for excellently preserved tetrapod trackways in the sandstones of the Tambach Formation since about 1885 (Pabst, 1896, 1908; Mueller, 1954, 1969; Haubold, 1971, 1973).

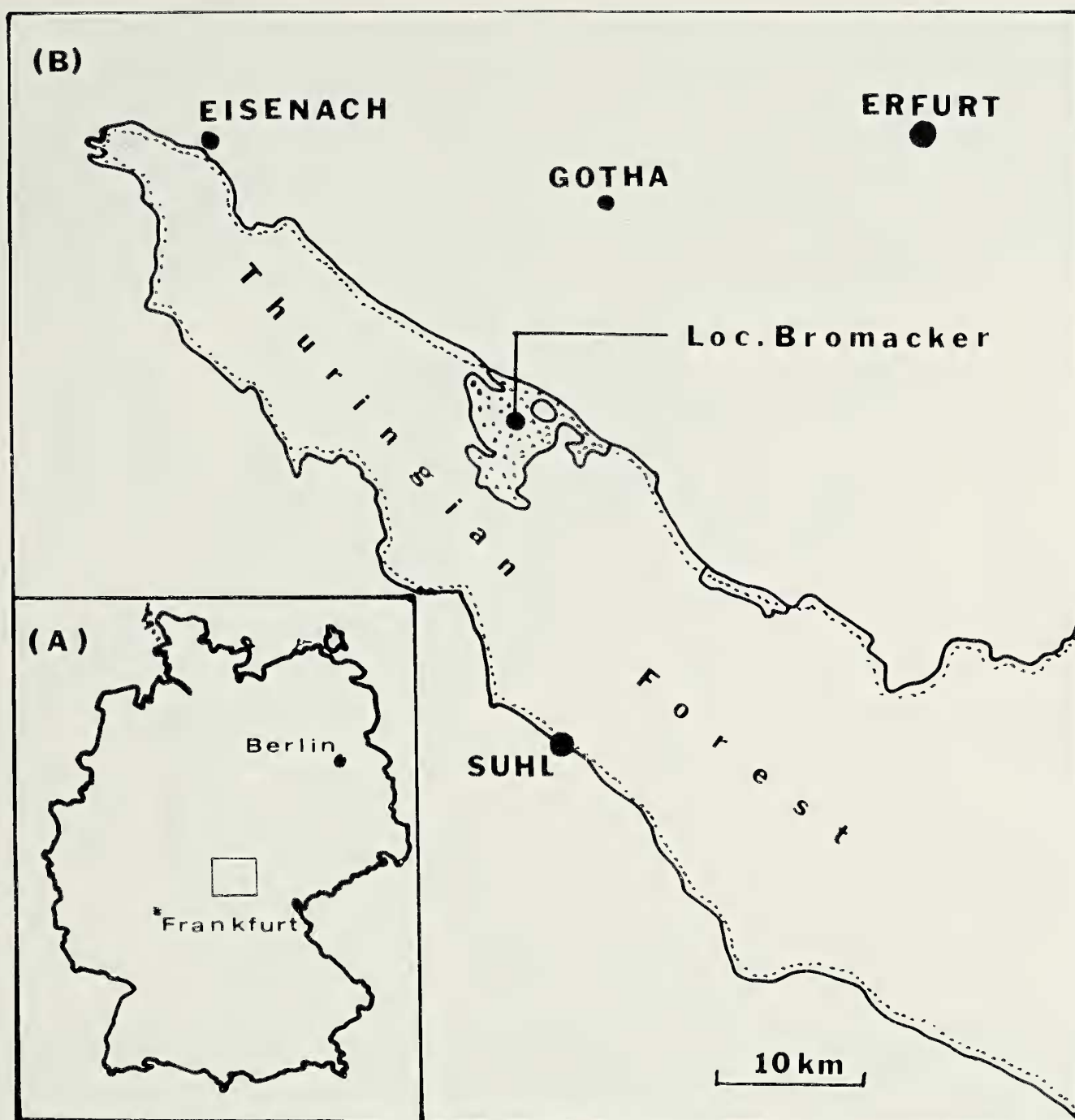


Fig. 1.—(A) Map of Germany with inset to show Thuringian Forest area. (B) Detailed map of the inset of (A) showing Bromacker locality and surrounding extent of Tambach Formation.

The stratigraphic section in the Thuringian Forest includes a succession of terrestrial formations of the Upper Carboniferous Stephanian and Lower Permian (Lower and Upper Rotliegend) that lies disconformably on crystalline basement rocks of the Hercynian orogen and are overlain in places by the Upper Permian marine Zechstein. The Stephanian-Rotliegend sediments of the Thuringian Forest were deposited in an intramontane basin sometimes referred to as the Thuringian Forest Basin. This basin, however, is actually the southwestern portion of a larger, northeast-trending basin, the Saale Basin, which extends about 200 km to the northeast to also include the Halle Basin. Upper Carboniferous and Lower Permian deposits of the Saale Basin, as well as other intramontane basins of central and western Europe, originated from the erosion of the rising Hercynian orogen and the filling associated with subsiding depressions and fault blocks. It is important to note that the Rotliegend, as well as its subdivision into lower and upper units, is a traditional lithostratigraphical unit that refers to continental beds of uppermost Carboniferous and Permian age in central Europe. In western Europe

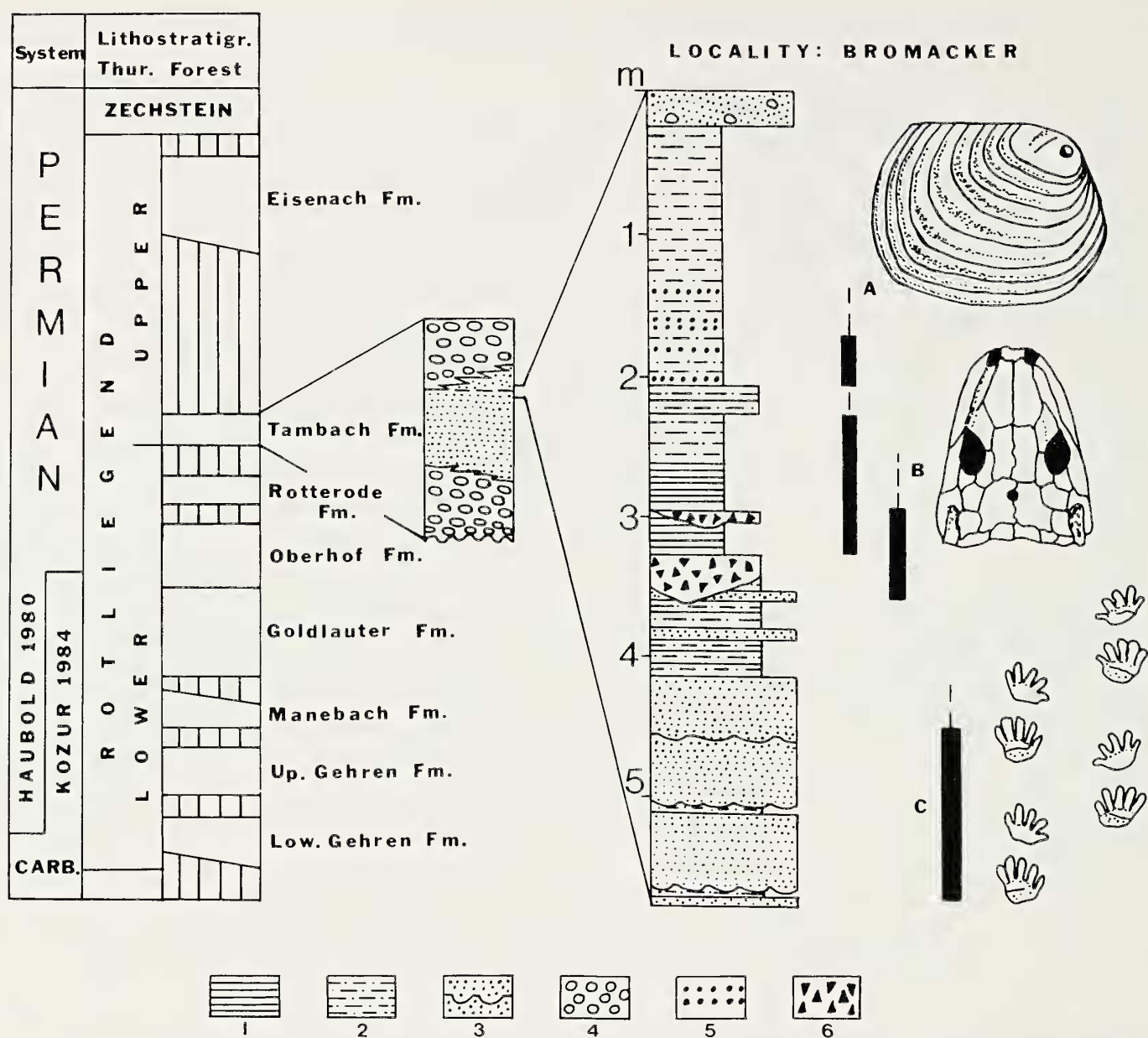


Fig. 2.—Generalized lithostratigraphic model of the Permo-Carboniferous of the Thuringian Forest area of central Germany. Levels of the Permo-Carboniferous boundary proposed by Haubold (1980) and Kozur (1984) are indicated. Lithofacies of the Tambach Formation in general and of the exposed section at the Bromacker locality in detail are shown; indicated lithofacies include: 1, laminated siltstone; 2, siltstone; 3, fine-grained sandstone with mudcracks; 4, conglomerate; 5, calcareous concretions; 6, clay-pebble conglomerate. Vertical bars A, B, and C indicate levels of occurrences of conchostracans, tetrapod skeletons, and tetrapod trackways, respectively.

the lithostratigraphic terms Autunian (derived from the Permian basin near Autun, France) and Saxonian (derived from the Sachsen-Anhalt region in central Germany) are used commonly to replace Lower and Upper Rotliegend, respectively.

Exposures at the Bromacker locality (Fig. 2) are limited to the Tambach Formation, which is the lowermost formational unit of the Upper Rotliegend in the Thuringian Forest. The Tambach Formation consists of typical red-bed fluvial deposits that can be divided into three major units: a basal conglomerate unit, an approximately 60 m thick middle sandstone unit, and an overlying typical fanglomerate unit. Only the uppermost level of the middle sandstone unit is exposed in the Bromacker quarry. Within this level a general sequence of three distinct fluvial facies can be recognized, each containing particular types of fossils. The lower third of the section consists of thick-bedded sandstones. They contain

thin intercalations of silty mudstones that originated from (?seasonal) floods and possess mudcracks and tetrapod trackways. In the middle portion of the section are flat-bedded channel fills consisting mainly of mudstones containing clay-pebble conglomerates. These channels contain the tetrapod skeletal remains discussed in this report. The upper half of the section consists of shaly siltstones, in part laminated and rich in mica, with layers of lenses of fine-grained sandstones. They were deposited on a fluvial floodplain with ephemeral bodies of quiet water and contain layers rich in conchostracans and some remnants of insects.

#### SYSTEMATIC PALEONTOLOGY

Order Batrachosauria

Suborder Seymouriamorpha

Family Seymouriidae

Genus *Seymouria* Broili, 1904

*Seymouria* cf. *S. sanjuanensis* Vaughn, 1966

*Specimens.*—This study is based on two specimens of *Seymouria*. One, MNG 7727, consists of the greater part of a skull, measuring about 56 mm in length, with both jaws closely attached, and isolated but closely associated right clavicle and ilium (Figs. 3–8). MNG 7727 was discovered in 1986 and identified as *Seymouria* in subsequent reports by Martens (1988, 1989). The second and much smaller specimen, MNG 8759, is reported here for the first time. It is a partial, articulated skeleton consisting of a complete skull, measuring about 21 mm in length, with closely applied jaws, shoulder girdle, and partial forelimbs.

*Horizon and locality.*—Uppermost level of 60 m thick middle sandstone unit of the Lower Permian Tambach Formation, Upper Rotliegend, in the Bromacker locality of the middle part of the Thuringian Forest near the village of Tambach-Dietharz and about 20 km south of the town of Gotha, central Germany. The German specimens are compared with those of *S. sanjuanensis* and *S. baylorensis* from the Lower Permian of the southwestern United States and some confusion may arise regarding the stratigraphic levels of those specimens from Texas, because the previously and long-used scheme of formational names (Plummer and Moore, 1921; Romer, 1974) has been recently revised by Hentz (1988). Throughout the text, therefore, where there is a conflict between the two nomenclatures, the newer scheme is followed parenthetically by the older one.

#### DESCRIPTION AND COMPARISON

Unless otherwise stated the following description of the German *Seymouria* will be based on specimen MNG 7727, which consists of most of the skull with lower jaws, right clavicle and ilium (Fig. 3–8). The skull has undergone considerable dorsoventral flattening and undistorted would have probably had a rather box-like structure at least in the postorbital region, with the cheek and skull table joining at almost a right angle. Although most of the dermal roofing bones are represented, only the left side of the skull is nearly intact. Here the intertemporal was displaced a few millimeters dorsal to the skull roof and removed subsequently during preparation, and the tabular and postparietal are lost. The presence, shape, and relationships to adjoining bones of the left intertemporal are easily established, however, because the bones surrounding it have retained almost exactly their original positions. Of the right side of the skull roof, the premaxilla, nasal, greater part of the lacrimal, and anterior portion of the dentary are in place, the postfrontal,



Fig. 3.—*Seymouria* cf. *S. sanjuanensis* MNG 7727. Photograph showing skull in dorsal view.

jugal, and postorbital have been displaced a short distance and are exposed in internal view, and the frontal, parietal, postparietal, postfrontal, temporal series, squamosal, and quadratojugal are missing or simply cannot be identified among the jumble of bones just posterior to the skull.

All the sutures are open and very easily traced. The sculpturing is moderately developed and present in all areas where it would be expected. There are no indications of a lateral line structure except possibly for a pronounced, smooth groove along the orbital margin of the postorbital. It ends abruptly, however, at the margins of the bone. A similar channel is only vaguely recognizable in specimens of *S. sanjuanensis*. The approximately 56 mm overall length of the skull is quite small, only about 64% of that of the smallest known North American specimens (Berman et al., 1987). The small size, moderately developed sculptur-

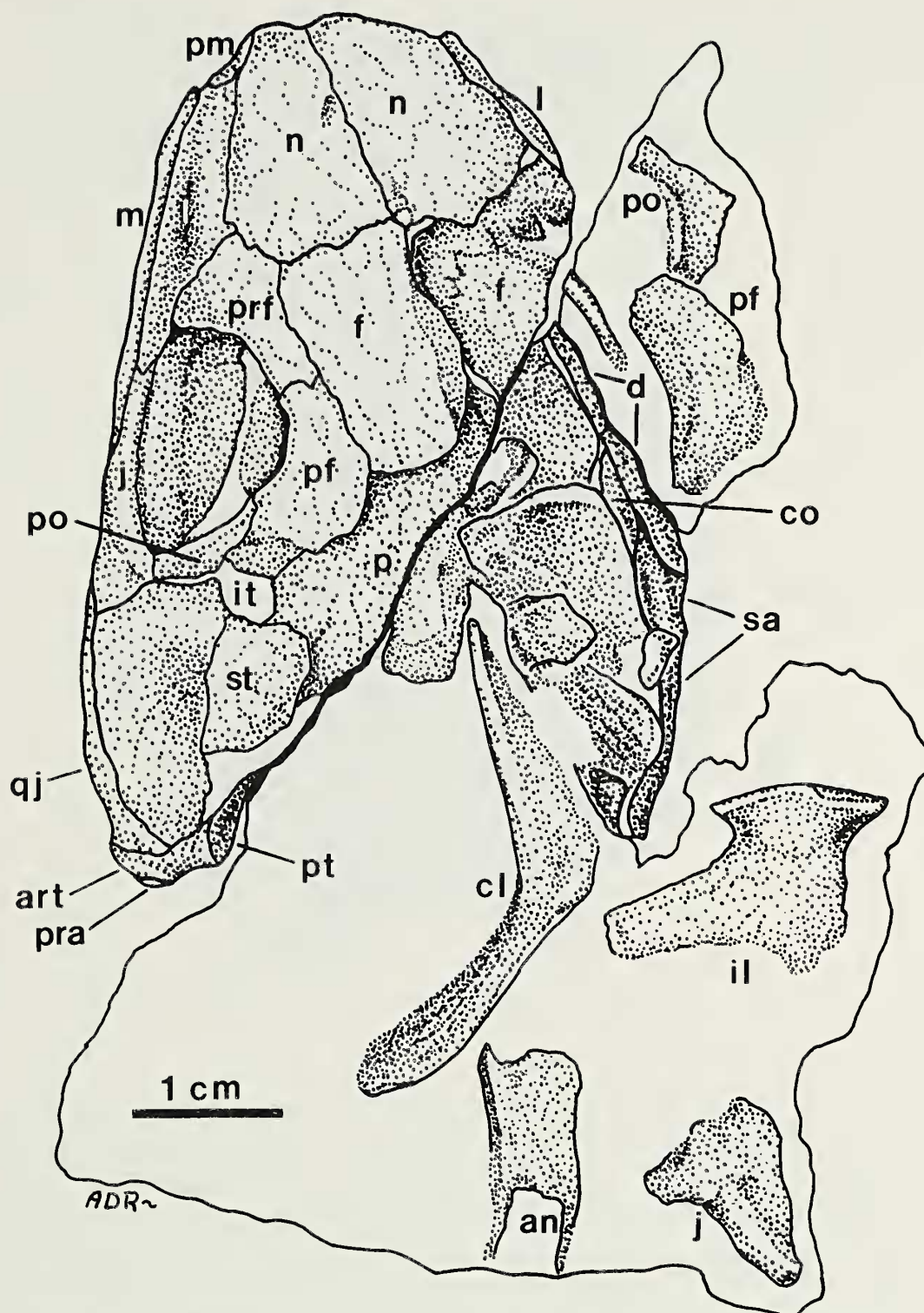


Fig. 4.—*Seymouria* cf. *S. sanjuanensis* MNG 7727, as seen in Fig. 3.

ing, open sutures, and postmortem movement of many skull roof elements suggest that MNG 7727 was probably not fully matured. The other *Seymouria* specimen from Germany, MNG 8759, is much smaller, with an overall skull length of only 21 mm. The dermal bones of the skull and shoulder girdle are very poorly ossified, lack sculpturing, appear often as a thin veneer or impression, and are commonly loosely or narrowly disarticulated; the limb elements are also very poorly ossified and exhibit no detailed structure. These features strongly suggest that MNG 8759 represents a very immature stage of development, probably postlarval.

Enough of the skull of MNG 7727 is preserved to see that it very nearly duplicates the anatomy of *S. sanjuanensis* and to a lesser degree that of *S. baylorensis*. The two other described species of *Seymouria*, *S. grandis* (Olson, 1979) and *S. agilis* (Olson, 1980), though poorly known, exhibit features that readily



Fig. 5.—*Seymouria* cf. *S. sanjuanensis* MNG 7727. Photograph showing skull in ventral view.

distinguish them as distantly related and are, therefore, not considered here. In view of the availability of detailed descriptions with reconstructions of *S. sanjuanensis* (Vaughn, 1966; Berman et al., 1987) and *S. baylorensis* (White, 1939), the description given here will be limited primarily to a comparison of those features that provide a basis for taxonomic assignment of the German specimens.

Berman et al. (1987) recognized two derived cranial characters to distinguish *Seymouria sanjuanensis* from *S. baylorensis*, using primitive temnospondyls and batrachosaurs as outgroups for determination of character polarities. In *S. sanjuanensis* the postorbital differs in being a very narrow, chevron-shaped element, with the limbs of the chevron extending farther along the dorsal and ventral margins of the orbit and the posterior projecting apex partially separating the intertemporal and squamosal. In contrast, the postorbital in *S. baylorensis* is subrectangular with only a slightly convex posterior margin that barely projects between the intertemporal and squamosal, and contributes far less dorsally and ventrally to the orbital rim. The postorbital of MNG 7727 appears to be identical to that of *S. sanjuanensis* and, as in this species, the distal end of the dorsal limb of the left postorbital just reaches the dorsal margin of the orbit by encroaching along the orbital border of the prefrontal. The full extent of the ventral limb of the left postorbital, however, is not visible, as dorsoventral crushing of the skull has displaced it along the medial surface of the jugal. The isolated right postorbital, however, clearly shows that the dorsal and ventral limbs are subequal in devel-



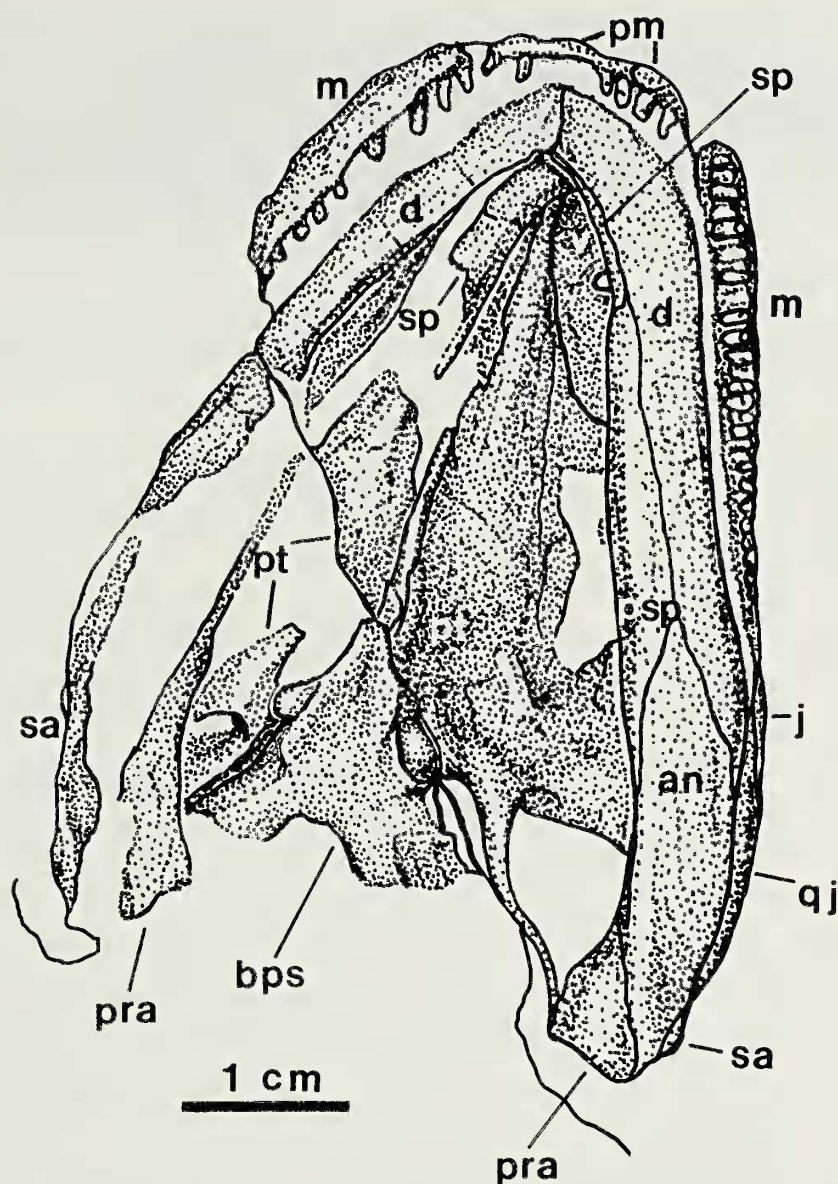


Fig. 6.—*Seymouria* cf. *S. sanjuanensis* MNG 727, as seen in Fig. 5.

opment. A second derived feature of *S. sanjuanensis*, the separation of the maxilla and quadratojugal by the jugal along the ventral margin of the dorsal skull roof, also occurs in MNG 727. The loss of contact between these two bones in *S. baylorensis* is apparently accomplished by a reduction in the anterior extent of the quadratojugal, rather than the posterior extent of the maxilla. In *S. baylorensis* the quadratojugal reaches to about the level of the midlength of the orbit, whereas in *S. sanjuanensis* and MNG 727 it extends anteriorly to only just beyond the posterior border of the orbit.

Several primitive features that separate *Seymouria sanjuanensis* from *S. baylorensis* were interpreted by Berman et al. (1987) as stages in morphological trends in *Seymouria*. Two of these are difficult to interpret in MNG 727 because of the incompleteness of the skull. A diagnostic feature originally used by Vaughn (1966) to distinguish the Utah specimens he assigned to *S. sanjuanensis* from *S. baylorensis* and later also utilized by Berman et al. (1987) in assigning New Mexico specimens to the same species was the greater anteroposterior extent of the postparietals. This feature was measured as the percent of the total length of the skull occupied by the postparietals. In *S. sanjuanensis* the postparietals are 10.2–11.1% of the skull length, whereas in *S. baylorensis* they are 8.9–9.6% (Berman et al., 1987). Though the postparietals are absent in MNG 727, a restoration of this



Fig. 7.—*Seymouria* cf. *S. sanjuanensis* MNG 7727. Photograph showing skull in lateral view.

area of the skull table that assumes no radical differences from those of either species yields a value (Table 1) slightly greater and, therefore, closer to that for *S. sanjuanensis* than for *S. baylorensis*.

Differences in the structure of the supratemporal and tabular also distinguish the two species. In *S. baylorensis* the posterolateral corner of the supratemporal and the adjacent lateral margin of the tabular are greatly expanded as a well-developed process that is bent sharply ventrally and sculptured externally. Anterior to and continuous with the downturned process of the lateral margin of the supratemporal is a narrow, vertical otic shelf that projects from the lateral margin of the ventral surface of the supratemporal. Its smooth external surface is continuous with that of the squamosal bordering the otic notch. On the other hand, in *S. sanjuanensis* the same process of the supratemporal and tabular is only slightly developed and extends only slightly ventrolaterally. The smooth, vertical otic shelf of the supratemporal extends to the posterolateral corner of the bone. Although the tabular is missing in MNG 7727, the supratemporal is complete and exhibits only the slightest indication of a laterally downturned process of its posterolateral corner. The smooth, vertical otic shelf of the supratemporal tapers posteriorly to a point as it nearly reaches the end of the slightly downturned, posterolateral corner of the bone.

Four closely related differences of the maxilla and its dentition not only distinguish between *Seymouria sanjuanensis* and *S. baylorensis*, but also demonstrate that the former is more primitive (Berman et al., 1987). These differences were interpreted as representing morphological trends in the genus and include: 1) reduction in the number of teeth, 2) overall increased size of the teeth, 3) increased heterodonty of the "canine" region, and 4) increased height of the maxilla. Berman et al. (1987) presented a series of four groups of *Seymouria* specimens to illustrate these trends that included, arranged in order of increasing degree of advancement

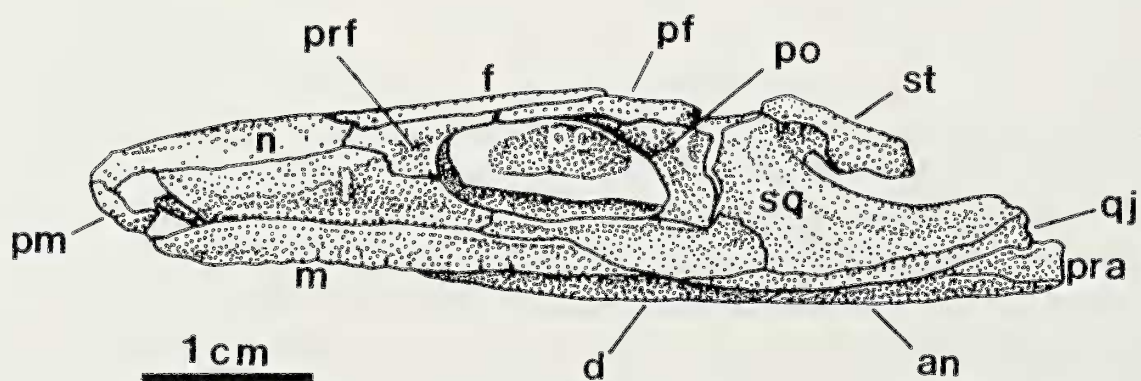


Fig. 8.—*Seymouria* cf. *S. sanjuanensis* MNG 7727, as seen in Fig. 7.

Table 1.—Comparative skull dimensions (in mm) of specimens of *Seymouria*. Those for *S. sanjuanensis* from New Mexico (CM 38022, 28596, 28597) and Utah (NTM VP 1023, 1024, 1025, 1034) and *S. baylorensis* from Texas (CNHM 663; MCZ 1081, 1082, 1083, 1085) except TMM 31189-1 are given as averages based on data from Berman et al. (1987). All proportions are given as percentages. Abbreviations: e, estimated; MxD, maxillary depth; MxL, maxillary length; MxT, number of maxillary teeth; PpL, postparietal length; SkL, skull length.

Specimens	SkL	PpL	$\frac{PpL}{SkL}$	MxD	MxL	$\frac{MxD}{SkL}$	MxT	$\frac{MxL}{MxT}$ SkL
<i>Seymouria sanjuanensis</i>								
New Mexico	89	9.3	10.5	7.7	51	8.5	29	2.0
Utah	89	10.0	11.1	10.0	51	11.0	25	2.3
<i>Seymouria baylorensis</i>								
Texas, TMM 31189-1	99	9.3	9.4	9.8	58	10.0	21	2.8
Other Texas specimens	111	10.5	9.3	15.0	60	13.5	17	3.2
<i>Seymouria</i> cf. <i>S. sanjuanensis</i>								
MNG 7727	56	e7.0	12.5	3.7	30	6.6	24	2.2

and general stratigraphic sequence from the lowest occurrence: 1) *S. sanjuanensis* specimens from the early to middle Wolfcampian (earliest Permian) age Cutler Formation of New Mexico (Berman et al., 1987); 2) *S. sanjuanensis* from the late Wolfcampian age Organ Rock Shale, Cutler Group of Utah (Vaughn, 1966, 1970; Blakey, 1980); 3) *S. baylorensis* skull TMM 31189-1 from the latest Wolfcampian age Nocona Formation (Admiral Formation), Wichita Group of Texas. Though this specimen is intermediate between *S. sanjuanensis* and *S. baylorensis* in several characters, Berman et al. (1987) referred it to the latter species on the basis of its closer overall form; it is, therefore, the only Texas specimen of *S. baylorensis* represented by good cranial material not from the Clear Fork Group; and 4) *S. baylorensis* specimens from the middle Leonardian age, lowermost level of the Clear Fork Group (Arroyo Formation) of Texas (Williston, 1911; White, 1939). Measurements expressing the trends of the dentary and its dentition are given in Table 1 as averages for each of the four groups of *Seymouria* specimens listed above (based on data from Berman et al., 1987) and the German specimen MNG 7727.

Of the upper marginal dentitions, only those of the premaxillae and left maxilla are complete in MNG 7727. As in *Seymouria sanjuanensis* and *S. baylorensis*, the premaxilla of MNG 7727 possesses, or has spaces for, six subequal teeth, but as expected they are considerably smaller, having a maximum length of about 1.8 mm and a maximum basal diameter of about 1.0 mm. The complete left maxilla of MNG 7727 possesses 25 teeth, or tooth positions, which equals the average value for specimens of *S. sanjuanensis* from the late Wolfcampian of Utah, but is well above those values for specimens of *S. baylorensis*.

Following Vaughn (1966), Berman et al. (1987) employed two sorts of calculations to demonstrate differences in the relative developments of the maxillary dentitions of specimens of *S. sanjuanensis* and *S. baylorensis*. One calculation used was the percent ratio of the average unit length of the maxilla per tooth to overall skull length. As indicated in Table 1, there is a marked separation between the average values for specimens of *S. sanjuanensis* and *S. baylorensis*; MNG 7727 lies within those of the former. Differences in the relative sizes of individual teeth of the maxillary dentitions of *S. sanjuanensis* specimens CM 28596 from

New Mexico and NTM VP 1034 from Utah, and *S. baylorensis* specimens TMM 31189-1 and MCZ 1028 from Texas were also depicted graphically by plotting the ratio of their basal diameters (rather than tooth length since crowns are seldom preserved) to skull length. The advantage of this measurement is that it allows a direct comparison of the relative development of not only the dentitions in general, but of specific regions. The values obtained for the largest "canine" tooth of the maxillary series of each of the above specimens were 0.020, 0.017, 0.033, and 0.040, respectively, indicating a noticeable increase in the relative sizes of the teeth in the "canine" region. The same measurements for the eleventh tooth of the same series of maxillae are 0.010, 0.012, 0.022, and 0.026, respectively, indicating not only that the cheek teeth of *S. sanjuanensis* are relatively smaller than those of *S. baylorensis*, but also that in this series of specimens the rate of increase in the relative sizes of the cheek teeth is less than that of the "canine" teeth. Applying the same method of calculating relative tooth size to the German *Seymouria* MNG 7727, the largest tooth of the "canine" region, the fifth, has a value of 0.018 and the eleventh tooth 0.011. These values are essentially the same as those for the *S. sanjuanensis* specimens CM 28596 and NTM VP 1034.

As would be expected, with the increased development of the maxillary dentitions in the *Seymouria* species of North America there is a general increase in the depth of the maxilla to accommodate them, particularly at the level of the "canine" region. In Table 1 this is expressed as the percent ratio of the maximum depth of the maxilla to the total skull length. Although the separation of values for the two species of *Seymouria* is not decisive due primarily to the intermediate value for *S. baylorensis* specimen TMM 31189-1, *S. sanjuanensis* is clearly the more primitive species in this feature. The value for MNG 7727 is slightly lower and, therefore, may represent a more primitive state of development.

There is one other difference between specimens of *Seymouria sanjuanensis* and *S. baylorensis* that has not been described in earlier comparisons. Casual inspection of the sutural patterns of the skulls of both species indicates a consistent difference in the relative positions of the anteriormost extents of the squamosals, intertemporals, and parietals. In *S. sanjuanensis* these bones reach, nearly reach, or extend just beyond the level of the posterior border of the orbit, whereas in *S. baylorensis* they end well behind the orbits. These two sutural patterns appear to reflect a difference in the relative elongation of the skull that is confined to a narrow, transverse band immediately posterior to the orbits. The difference in the relative elongation of the skull in this region can be demonstrated by expressing the distance between the otic notch and the orbit as a percent ratio to skull length. Though the differences between the average values of about 14.4 (range approximately 12.5–16.7) for the New Mexico and Utah specimens of *S. sanjuanensis* and 18.5 (range approximately 17.4–19.1) for the Texas specimens of *S. baylorensis* is small, they do not appear to overlap. On the basis of the general condition in primitive temnospondyls and batrachosaurs, the shorter postorbital region with a more forward position of the squamosals, intertemporals, and parietals in *S. sanjuanensis* is considered primitive. Although there has been some displacement of the skull elements in the postorbital region of the German specimen MNG 7727, it appears to duplicate *S. sanjuanensis* in this feature, with an estimated value for the above calculation of 12.3.

Near the upper margin of the left orbit in MNG 7727 is a large, semicircular plate of bone that appears to represent part of a palpebral cup. This structure has not been previously described in *Seymouria*.

The palate of MNG 7727 is partly obscured by the closely attached jaws, and that which is visible is badly fractured, with portions missing or slightly displaced. A greater portion of the left side of the palate is exposed, but only the suture separating the pterygoid and vomer is detectable. Only the crown of the vomerine tusk is visible, protruding medially above the splenial of the lower jaw (Fig. 5, 6). As in all species of *Seymouria*, the palate is completely closed by the pterygoids and vomers, which are covered by a shagreen of teeth. The pterygoid portion of the basiptyergoid articulation is formed by a well-developed, semi-hemispherical, cup-like structure that projects ventrally and is open medially and dorsally. Also as in other *Seymouria* species, the pterygoid is unusual in forming a straight, transverse anterior border of the subtemporal fossa. With the exception of the shagreen teeth, these features of the palate are preserved in the smaller German skull MNG 8759.

The only identifiable portion of the braincase of MNG 7727 is an essentially complete basiparasphenoid complex; the jumble of mainly unidentifiable elements at the posterior margin of the skull may include other portions of the braincase. The basiparasphenoid conforms very closely to that in *Seymouria* except for one seemingly obvious difference, the structure of the cultriform process of the parasphenoid. White (1939) described the cultriform process in *S. baylorensis* as being a very short, broad, triangular process in ventral view, extending only about 15 mm beyond the basiptyergoid processes and contacting along its lateral margins the pterygoids to help close the interptyergoid vacuity. This appears to be the same structure of the parasphenoid seen in *S. sanjuanensis*. The cultriform process of MNG 7727 is identical to that of both *Seymouria* species except for a narrow, additional distal portion that approximately doubles the relative length of the process. The anterior portion of the process has the typical V-shaped cross-section, with the apex directed ventrally. Though the palate is poorly preserved, it can be seen that at least in some places the pterygoids partially overlapped the ventrolateral margins of the process. Therefore, it is not certain whether the anterior portion of the cultriform process in MNG 7727 would be visible in an undisturbed specimen. The presence of a long cultriform process in MNG 7727, if actually absent in other *Seymouria* species, would set it apart as more primitive. Posterior to the basiptyergoid processes the parasphenoid in *Seymouria* forms greatly expanded, lateral wings that cover the anterior half of the ventral surface of the otic capsule (White, 1939). Only the right lateral portion of the parasphenoid is complete in MNG 7727, and, though it exhibits a similar extensive outward expansion, its full extent anterolaterally is obscured by the quadrate ramus of the pterygoid. The midline portion of the parasphenoid between the posterolaterally diverging cristae ventrolaterales is apparently incomplete.

The lower jaws are in place and closely appressed to the outer margins of the palate and have rotated slightly on their long axis so that the lateral surface faces ventrally. The left jaw is complete, whereas in the right the region of the splenial and postsplenial is incomplete and slightly displaced and the incomplete angular lies a short distance behind the skull. It is not possible to expose the dorsomedial margin, including the adductor fossa, of either jaw; the dorsolateral margin and its dentition of each jaw is also hidden from view except for the posterior end of the right jaw. This exposure results from the absence of the cheek area of the skull roof. Features of the exposed areas of the jaws are well preserved and exhibit no noticeable deviations from the description given by White (1939).

The isolated right clavicle and ilium are located directly behind the skull. The

clavicle is complete and exposed in dorsal and medial views; it exhibits no noteworthy differences from that of *Seymouria* except for possibly the ventral spatulate blade being relatively slightly narrower in anteroposterior breadth. The nearly complete ilium is exposed in medial view and only the thin dorsal margin of the dorsal blade is incomplete. As in *Seymouria*, there is a well-developed posterior process, but that in MNG 7727 differs slightly in having a narrowly rectangular rather than triangular outline and in being directed posterodorsally rather than posteriorly.

#### SYSTEMATIC PLACEMENT

The German *Seymouria* specimens very closely duplicate the anatomy of *S. sanjuanensis* and, therefore, are easily distinguished from *S. baylorensis*. The German form, however, does appear to exhibit one feature that distinguishes it from the two above species, the primitive possession of a long narrow cultriform process of the parasphenoid. All of the minor differences from *S. sanjuanensis* discussed above may reflect an immature stage of development of the German specimens rather than specific differences. Until more complete specimens of the German form can be studied, it seems best not to create a new species on the basis of one primitive feature. For these reasons the German *Seymouria* MNG 7727 and 8759 are referred to *S. sanjuanensis*.

#### DISCUSSION

In addition to *Seymouria*, three other tetrapod taxa have been described or identified from the Bromacker locality on the basis of good skeletal remains. Boy and Martens (1991) described a new genus of protorothyridid captorhinomorph, *Thuringothyris mahlendorffae*, whereas other specimens were tentatively identified by Martens (1988, 1989) as amphibians belonging to the families Trematopidae and Limnoscelidae. Also discovered recently but not reported from the Bromacker locality is a skull of a diadectomorph amphibian that is very close to *Diadectes*, if not congeneric, and is presently being studied by the authors. As in the case of *Seymouria*, trematopids, diadectid and limnoscelid diadectomorphs, and captorhinomorphs have not previously been reported, at least not on the basis of substantial evidence, from any other locality in the Rotliegend or its equivalents in France or England. At least two explanations can be offered for the absence of representatives of these taxa elsewhere in the Lower Permian of central and western Europe.

Poor exposures and the long-standing, widely accepted misconception that the red beds of the Upper Rotliegend represent an inhospitable dry climate in which the preservation of vertebrate skeletal remains would have been unlikely have combined to foster a history of little interest in their exploration. This has had the expected result of there being only a very small number of vertebrates collected from the Upper Rotliegend. Alternatively, most investigators have concentrated on the lacustrine grey sediments and black shales of the Lower Rotliegend in which are found such well-known tetrapod localities as Niederhaesslich, Friedrichroda, and various Saar-Nahe sites such as Lebach. These sediments have produced a preponderance of obligatory aquatic amphibians, particularly those of the larval "branchiosaur" amphibians. On the other hand, representatives of a terrestrial or semi-terrestrial fauna preserved as skeletal remains from the Rotliegend and its equivalents (Autunian and Saxonian) in France and England are widely scattered and quite rare. These include the microsaur amphibians *Saxo-*

*nerpeton* and *Batropetes* (Carroll and Gaskill, 1978; Carroll, 1991), the possible diadectid ?amphibian *Phanerosaurus* (Geinitz and Deichmueller, 1882), the pelycosaur reptiles *Haptodus* (Paton, 1974; Currie, 1979), *Ophiacodon* (Paton, 1974), *Edaphosaurus* (Jaekel, 1911), *Sphenacodon* (Paton, 1974), and *Casea* (Sigogneau-Russell and Russell, 1974), and the questionable araeoscelid diapsid reptile *Kadaliosaurus* (Credner, 1889). Of the above list, however, only specimens of the pelycosaurs *Haptodus*, *Ophiacodon*, *Sphenacodon*, and *Casea* from France and England were recovered from red-bed deposits.

The Bromacker locality is, therefore, unique among Rotliegend or equivalent deposits in central and western Europe for its high representation of terrestrial or semi-terrestrial vertebrates. This aspect of the assemblage will undoubtedly increase as more skeletal remains from the Bromacker locality are studied. In this regard it is worth noting that trackways from the sandstone units of the Tambach Formation (Pabst, 1896, 1908; Haubold, 1971, 1973; Boy and Fichter, 1988) and other Rotliegend localities indicate a diverse terrestrial tetrapod fauna, including pelycosaurs. Despite the presently limited picture of the Bromacker assemblage, it clearly indicates a very close alliance with those of the Lower Permian red-bed deposits of the Dunkard Group of the eastern United States (Romer, 1952; Berman and Berman, 1975; Olson, 1975) and, particularly, the southwestern United States (Olson and Vaughn, 1970). The apparent explanation for the similarity between the widely separated Lower Permian red-bed tetrapod assemblages of the Bromacker locality and those of the United States is that similar environments are being sampled. This, in turn, would suggest that barriers to faunal interchange between these widely distant regions could not have been strong, though regional differences would be expected.

Although there is no doubt that the Bromacker vertebrate assemblage indicates a Lower Permian horizon for the Tambach Formation of the Upper Rotliegend of the Thuringian Forest in central Germany, the presence of *Seymouria* specimens referable to *S. sanjuanensis* strongly suggests an earliest Permian age of Wolfcampian.

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